FLORAL STRUCTURE AND ANATOMY IN THE FAMILY GOODENIACEAE DUMORT.

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(Forty-five Text-figures.)

[Read 29th July, 1959.]

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Synopsis.

The floral anatomy of most genera in this family has been examined. It is concluded that the ovary of the Goodeniaceae is 4-carpellary, although various reductions and fusions obscure this. The ovary is fairly constant in form; a basal 2-locular zone, a medial unilocular zone and an uppermost 2-locular zone, the latter two being sterile. The relative sizes of these zones give the appearance of partial or complete 1-locular or 2-locular conditions. Solidification of one loculus may also give an apparently 1-locular condition. The inferior condition of the ovary may, in general, be considered to have arisen by fairly superficial mass growth, i.e., by fusion of the outer floral parts to the ovary. The evolution within the family is considered in the light of these investigations. It is noted that floral form alone hardly indicates a Campanulaceous origin.

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INTRODUCTION.

The use of vascular patterns as a guide to structure has been a controversial technique. The crux of the problem appears to be the lack of knowledge of the fundamental cause of the initiation of a vascular strand. Puri (1951), Douglas (1944, 1957), and Eames and Macdaniels (1947) have summarized the arguments in favour of the conservative nature of vascular patterns. It is not intended to reiterate these arguments, suffice it to say that they appear reasonable. These patterns are controlled by the genotype of the plant and, because of their relative constancy, it can be assumed that the genetic systems responsible for them are well "buffered" against interference from the environment. The numerous cases of vascular strands pointing to the assumed positions of aborted organs implies that this genetic system is "conservative", i.e., new floral forms are superimposed on the previous vascular structures. Thus the vascular pattern of the flower can be used as a guide to changes in genotype, i.e., phylogeny.

Colozza (1907, 1908) has described the vegetative anatomy and Brough (1927) examined the ontogeny of the flower of a single species. Saunders (1939) gives some data on a few genera; this is not complete and the interpretation is coloured by the theory of carpel polymorphism. This theory is considered to be an unnecessary complication.

MATERIAL AND METHODS.

Mature flowers and often young fruits were embedded in wax in the usual manner using chloroform as the wax solvent. Both transverse and longitudinal sections were cut at a thickness of 15μ. The sections were stained with crystal violet and counter-stained with erythrosin. In most cases fresh material was fixed in formalin-acetic-alcohol. In a few cases herbarium specimens were soaked in warm detergent before embedding in wax. The results are presented as diagrams in the main; only a few of the drawings of the serial sections have been reproduced here. In view of the fact that a number of species are known to show variability in their floral vascular patterns (Hall, 1956) a number of specimens (between 5 and 15) were examined for each species. The nomenclature of the vascular strands is that used by Eames and Macdaniels (1947).

OBSERVATIONS.

The carpels appear to be considerably modified and the loculi walls are probably formed by several carpels. The term pseudocarpel is therefore used in this presentation of the results to include the walls of each loculus and the corresponding part of the septum (see below).

The point of reference for the genus may be taken as *Velleia* with a superior ovary and semi-epigynous stamens. This genus will be described rather more fully and the others compared with it.

VELLEIA Smith.

There are two main floral types within the genus, those with five sepals and those with three.

V. paradoxa R.Br. has five sepals. The first vascular strands which diverge from the central stele of the receptacle are on the sepal radii; almost immediately above these the strands on the petal radii also diverge and these latter almost immediately branch into three. The two lateral members of each group unite with the strands on the sepal radii, one on either side, whilst the central strand continues on into the petals without further change. Five further bundles diverge from the central stele on the
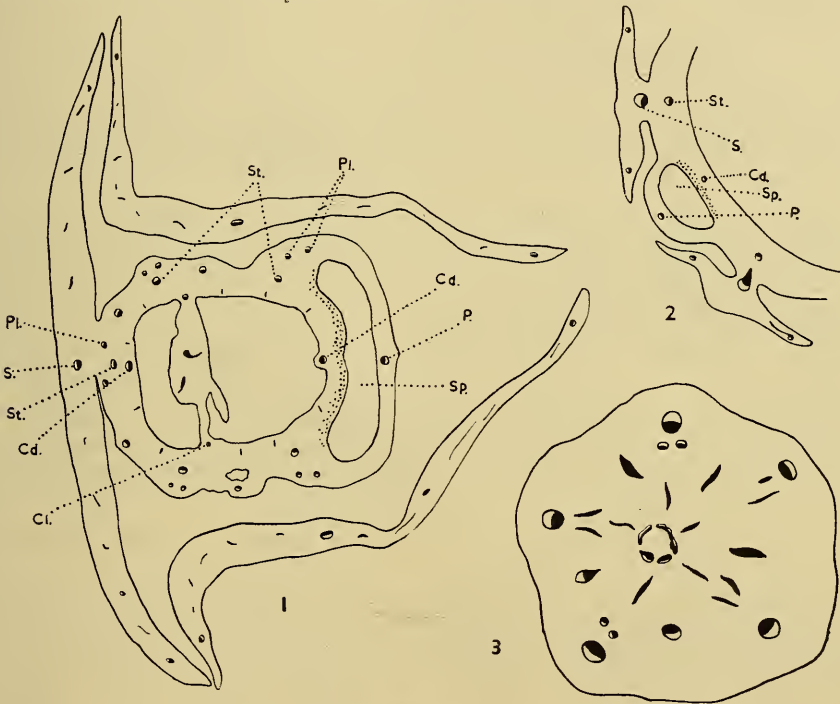
Text-figures 1-3.
1. *Velleia lyrata,* t.s. of lower flower. 2. *Goodenia scapigera,* part of pseudo-ovary. 3. *Goodenia decurrens,* t.s. of receptacle showing vascular strands before their fusion.

sepal radii (presumably the staminal bundles) which unite with those already on these radii (Fig. 3). The vascular elements remaining in the central stele resolve into four or five strands which further unite into two strands diverging outwards and a single strand in the centre. Those diverging outwards (pseudocarpellary dorsal bundles) are on the post.-ant. axis, the posterior one uniting with the posterior strand on the sepal radius and the anterior one doubling backwards into the spur. The outer floral whorls themselves are fused to the ovary at the base; the sepals become free first, except for the posterior one which remains united to the ovary for some considerable distance. In the lower quarter of the flower the petal lateral, staminal and post-pseudocarpellary dorsal bundles all diverge from the appropriate strand on the sepal radii, which latter passes into the sepal itself where it branches into three. The petals diverge somewhat higher up as a complete tube (Fig. 1, 2) into which the petal strands pass. Still higher the stamens diverge, also supplied by their own vascular

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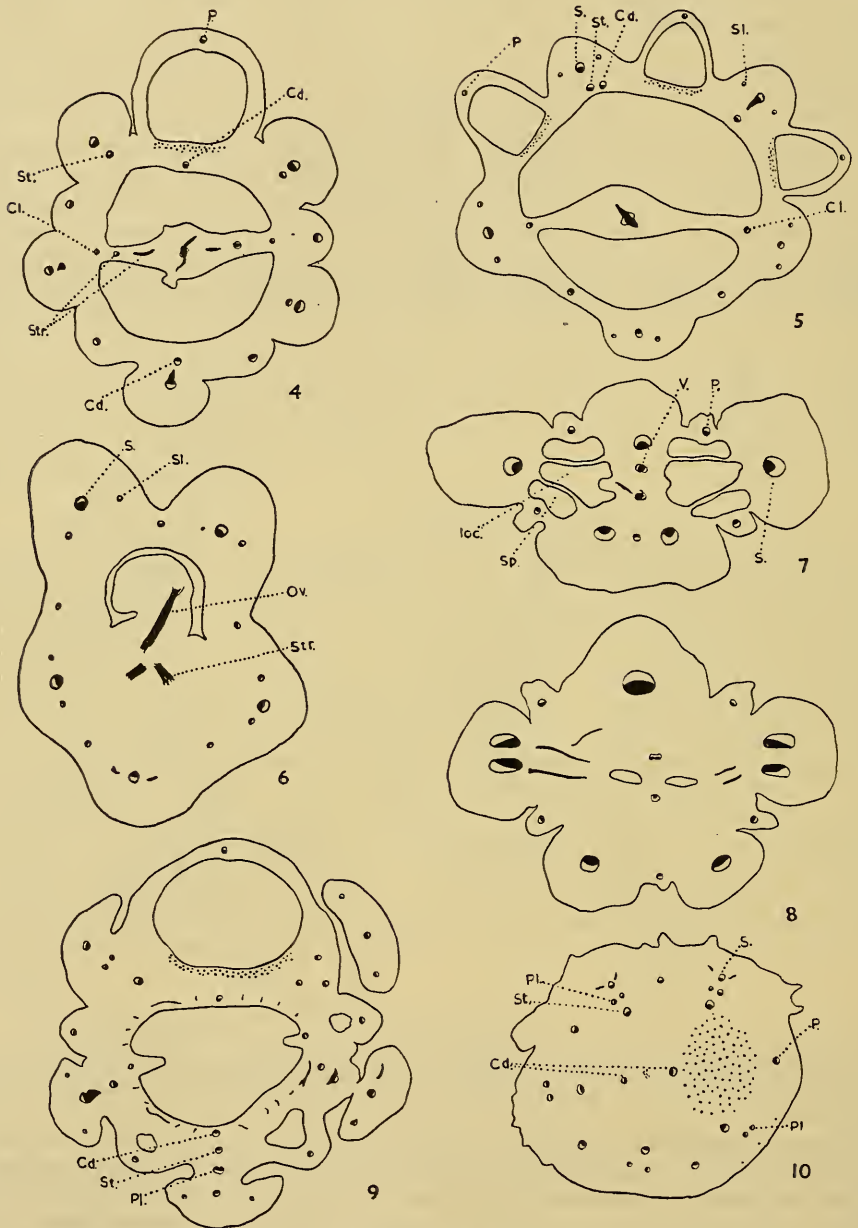
Text-figures 4-10.

4. *Goodenia decurrens*, t.s. of lower part of pseudo-ovary.   5. *Anthotium rubriflorum*, t.s. of pseudo-ovary.   6. *Dampiera stricta*, t.s. of pseudo-ovary at level of ovular insertion.   7. *Leschenaultia biloba*, t.s. of pseudo-ovary.   8. *Leschenaultia biloba*, t.s. of ovary dome. 9. *Goodenia decurrens*, t.s. of upper part of pseudo-ovary.   10. *Scaevola albida*, t.s. of ovary dome.

S, sepal main; Sl, sepal lateral; P, petal main; Pl, petal lateral; St, stamen; Cd, Ps-carp. dorsal; Cl, Ps-carp. lateral; V, Placental; Sp, spur or space.

supply (Fig. 3, 31). This fusion of the various vascular supplies and their subsequent separation from each other is illustrated in Figure 40, although in this case the separation occurs lower in the flower than in *Goodenia*. The anterior petal is drawn out into a spur whilst the anterior wall of the ovary is nectiferous. The remnants of the central stele pass into the placentae as an irregular bundle. Very low down two bundles pass out from it along the septum and take up a position at the junction of septum and ovary wall (ps.-carp. lat. bundles). The central bundle progresses up into the septum and branches of it supply the ovules. In addition two further sterile bundles pass out on either side towards the ovary wall and there fuse with the pseudo-carpellary lateral bundles (see Fig. 4). The remaining vascular tissues are entirely used up in supplying the uppermost ovules.

The ovary represents the standard Goodeniaceous type, the general form of which is repeated throughout the family. In the lowest part the ovary is divided by a single septum with an axile placenta (Fig. 1, 4). About halfway up the ovary a split appears in the axis, thus giving a semblance to parietal placentation (see Fig. 9). Very few ovules, or none at all, are inserted in this region; they are mainly found in the lower-most zone. Just below the ovary summit the inturned edges of the pseudocarpels meet once again, regenerating the apparently bilocular condition. Thus there is a lower-most "bilocular" zone, a medial "unilocular" zone and an uppermost "bilocular" zone (Fig. 31).

The style is supplied by the pseudocarpellary dorsal and lateral bundles which do not, however, pass into the style unchanged. They bifurcate as shown in Figure 11, and these branches fuse as indicated to give the condition of four bundles as shown in Figures 12 to 15. These four bundles are arranged over the loculi, none over the junction of septum and ovary wall as would be expected if the loculi represented individual carpels. Immediately below the indusium these bundles undergo a series of bifurcations to form a ring of vascular tissue.

V. lyrata R.Br.—This species has three sepals, but otherwise is very similar to the previous species. The lateral sepals are united to their anterior lateral partners and the vascular supply of these compound sepals still retains some degree of separateness (Fig. 1).

V. montana Hook. f.—Essentially the same as the preceding species.

SYMPHYOBASIS.

S. macroplectra (F. Muell.) Krause.—Unfortunately no material of this interesting monospecific genus was available. It would appear to be similar to *Velleia* except that the corolla and stamens are virtually epigynous, whereas the sepals are almost entirely hypogynous, i.e., the ovary is superior.
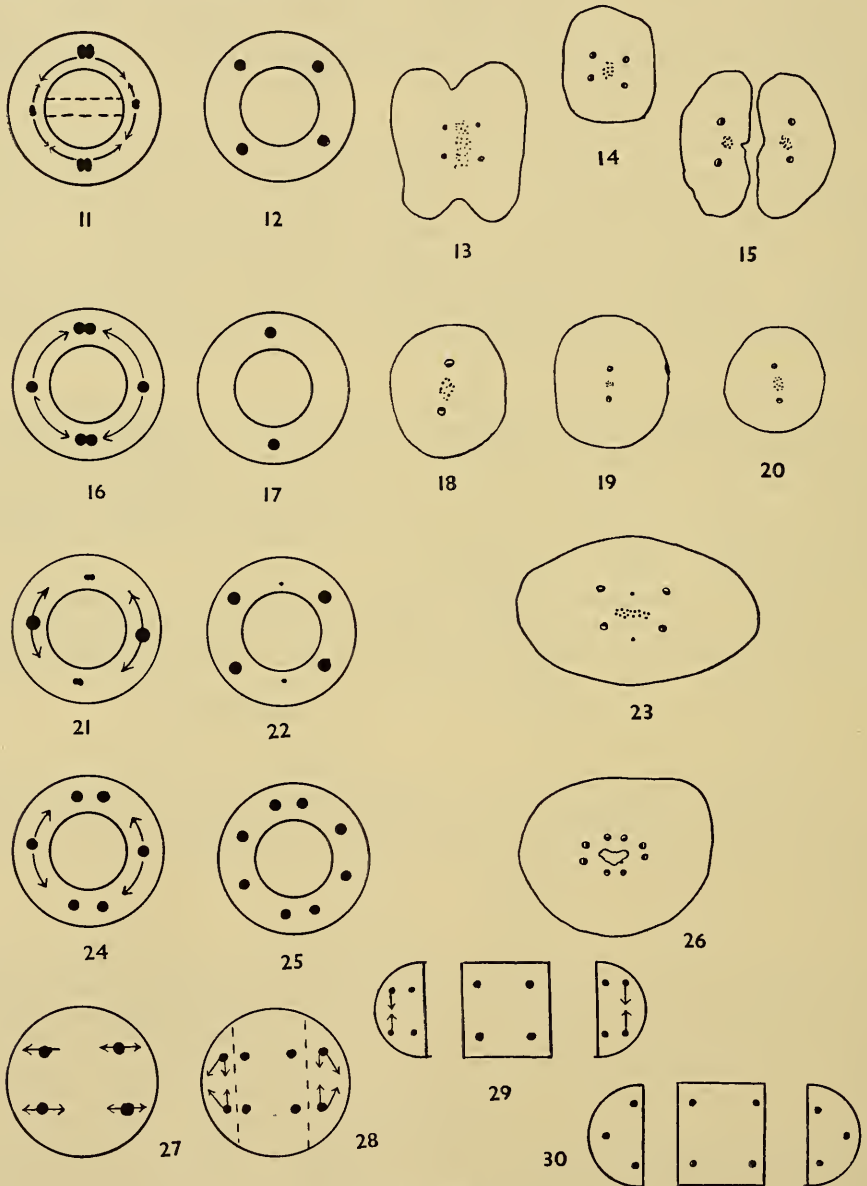
GOODENIA.

G. decurrens R.Br.—The basic plan is similar to that found in *Velleia paradoxa*. The sepals and other outer floral whorls separate from the ovary wall at a much higher level and the condensation of the vascular system is correspondingly increased (Fig. 4, 9, 32). The ribs on the floral tube each contain a bundle which divides at the point at which the rib diverges from the ovary wall as a sepal, into six as shown in Figure 40, although the bundle supplying the stamens may diverge somewhat lower (Fig. 4). These bundles are: sepal main, two sepal lateral, petal laterals and staminal. In addition the posterior bundle on the sepal radius gives rise to one of the pseudo-carpellary dorsal bundles (Fig. 40). These ribs have a different texture, and in some other species a different indumentum, from the grooves between them. The texture and the indumentum correspond exactly to that of the sepals which are formed by the separation of these ribs from the pseudo-ovary wall. The grooves are supplied with single bundles which pass directly into the petals as petal main bundles. The anterior pseudocarpellary dorsal bundle diverges from the bundle on the anterior petal radius at a low level in the pseudo-ovary wall and is separated from the ovary wall

proper by a spur or pocket (Fig. 4, 9, 32).   In other respects the vascular pattern is
similar to *Velleia* (also see Fig. 14, 40).

G. ovata Sm. and *G. bellidifolia* Sm. showed only minor differences.

G. heterophylla Sm.—In this species the sepals do not diverge from the pseudo-
ovary wall until very close to the summit of the ovary and there is a corresponding
condensation of the vascular tissue.

Text-figures 11-30.

11, 12. Derivation of stylar vasculation in 4-strand styles.   13. *Velleia paradoxa*, style.
14. *Goodenia bellidifolia*, style.   15. *Goodenia pusilliflora*, style.   16, 17. Derivation of stylar
vasculation in two strand styles (except *Brunonia*).   18. *Dampiera stricta*, style.   19. *Scaevola
hookeri*, style.   20. *Anthotium rubriflorum*, style.   21, 22, 23. Stylar vasculation of *Scaevola
ramosissima*.   24, 25, 26. Stylar vasculation of *Leschenaultia*.   27, 28, 29, 30. Vasculation of
stylar branches in *Calogyne pilosa*.   Varying levels in style; 27 lowest, 30 highest.

G. pusilliflora F. Muell.—Although agreeing with *G. decurrens* in most respects, the only specimens of this species which were examined had 2-fid styles. This branching reached almost to the base of the style and the cleft was at right angles to the ovary septum, each branch containing two vascular strands (Fig. 15) which have been formed in the same way as in *G. decurrens*.

G. paniculata Sm.—This species is a member of the Section Pluriseratim Benth. or Amphichila DC. The floral construction is similar to that of the other species described except that the ovules are inserted in a number of rows on the placentae instead of in two rows.

G. scapigera R.Br.—This species is a member of the section *Monochila* Benth. Once again it differs from the other species examined in minor details only, the most interesting being the attachment of the ribs (sepals) to the pseudo-ovary wall (Fig. 2). This attachment is by a narrow strip of tissue only; the whole inner surface of the sepaline rib is not adherent to the rest of the pseudo-ovary wall as in the previous species.

CALOGYNE.

C. berardiana (Gaudich.) F. Muell.—The floral structure of this species resembles that of the Goodenias very closely. The distinctive character is considered to be the 2-fid style, the structure of which is exactly similar to that of *G. pusilliflora* (see above).

C. pilosa R.Br.—This species differs from the Goodenias only in the presence of a 3-fid style. This branching occurs quite close to the indusium, the vascular supply of the branches being supplied by branches from the four standard bundles in the manner indicated in Figures 27–30. From these diagrams it is obvious that the stylar condition bears little relationship to that found in the previous species or to the carpellary condition of the ovary.

SELLIERA.

S. radicans Cav.—This genus has essentially the same floral structure as that found in the Goodenias. The sepaline ribs, however, are not evident as such and the pseudo-carpellary dorsal bundles separate from the corresponding outer bundles (see Figure 40) very low in the pseudo-ovary wall. The spur is reduced to a small anterior pocket.
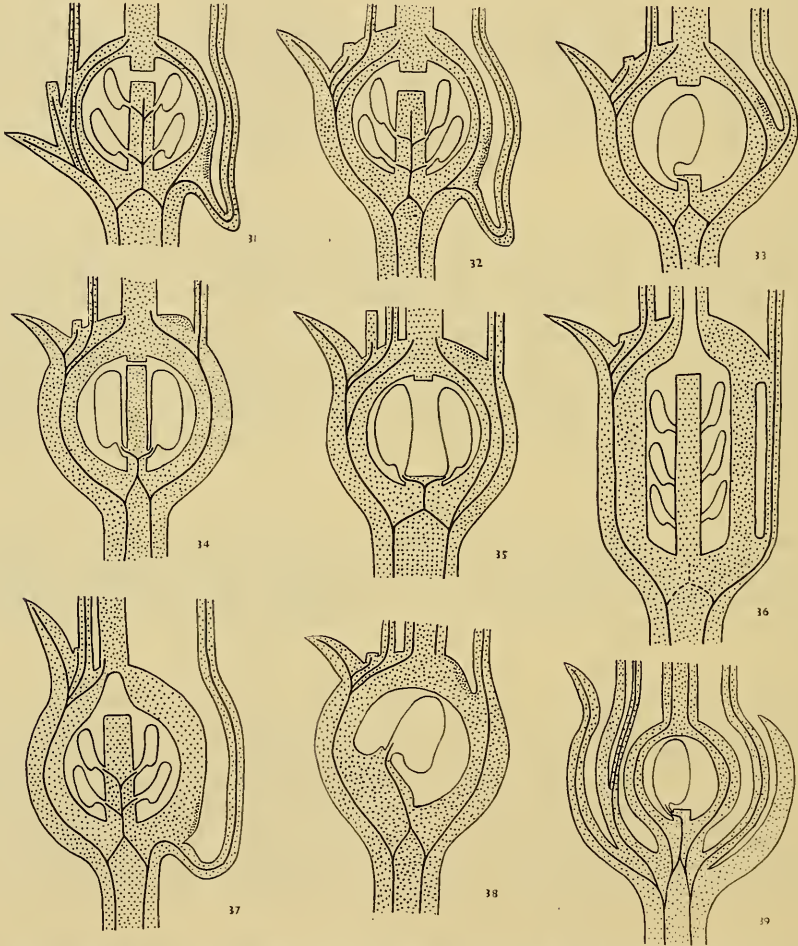
VERREAUXIA.

V. reinwardtii (de Vriese) Benth. The structure of the pseudo-ovary wall is essentially the same as that of the Goodenias (Fig. 33) and the derivation of the vascular supply of the separate organs is the same (see Fig. 40). The main difference is to be found in the ovary itself which is usually described as 1-locular with a solitary ovule. In fact the standard ovary form is present, but the lowermost "bilocular" zone and the uppermost "bilocular" zone are very small. The ovule is inserted in the posterior position on the short, lower septum. The sterile septal bundles do not occur, but otherwise the vascular pattern is similar to that found in the Goodenias (Fig. 33, 45).

SCAEVOLA.

Three main types of ovary are found in this genus as described by Krause (1912): (i) "bilocular" with one ovule per loculus; (ii) "unilocular" with two ovules in the loculus; (iii) "unilocular" with one ovule in the loculus.

S. albida Sm.—This species has type (ii) ovary, but once again it is found that the structure is really that of the generalized type as found in the previous genera. The basal "bilocular" zone is considerably reduced and one ovule is inserted on either side of the short septum. Immediately beneath the style the "bilocular" condition is regenerated. Ten bundles diverge from the central receptacular stele almost at the same time. These pass outwards into the pseudo-ovary wall unaltered. There are no ribs on the outside of this wall. Five of them on the sepal radii behave in the same way as those in the same position in *Goodenia*, the other five on the petal radii likewise

(Fig. 40, 10). There is, however, no spur and the anterior pseudocarpellary bundle diverges from the corresponding petal bundle at the summit of the ovary and not before (see Fig. 34). After the ten main bundles have diverged from the central stele the remnants resolve into a single bundle with irregular patches of phloem around a central xylem core. Below the septum, i.e., in the receptacle, this bundle branches into three, two passing outwards to the junction of septum and ovary wall (pseudocarpellary laterals) and the central one continuing into the placentae and supplying the ovules (Fig. 34).

Text-figures 31-39.   Longitudinal diagrammatic sections of pseudo-ovary.
31, *Velleia* ; 32, *Goodenia* ; 33, *Verreauxia* ; 34, *Scaevola (spinescens)* ; 35, *Diaspasis* ; 36, *Leschenaultia* ; 37, *Anthotium* ; 38, *Dampiera* ; 39, *Brunonia*.

S. spinescens R.Br.—This species has type (i) ovary.   Apart from the presence of an unvasculated septum extending almost to the top of the ovary there is little difference between this and the preceding species.   The basal "bilocular" zone is thus very large whilst the medial "unilocular" zone is very small (Fig. 34, 45).

S. hookeri F. Muell.—Similar to the previous species, but the style contains two vascular bundles derived as shown in Figures 16, 17 and 18.

S. ramosissima (Sm.) Krause.—This species displays a number of differences from the patterns described for the previous ones.   Generally the structure is the same as that found in *S. spinescens*, but the derivation of some of the vascular bundles at the ovary

dome is different. The sepal lateral bundles actually diverge from the bundles on the petal radii, a condition found nowhere else in the family so far. The pseudocarpellary dorsal bundles are very weak and when they reach the base of the style they do not bifurcate; the lateral bundles do, however, and the resultant bundles remain free. This produces a six-strand condition in the style of this species (Fig. 21–23).
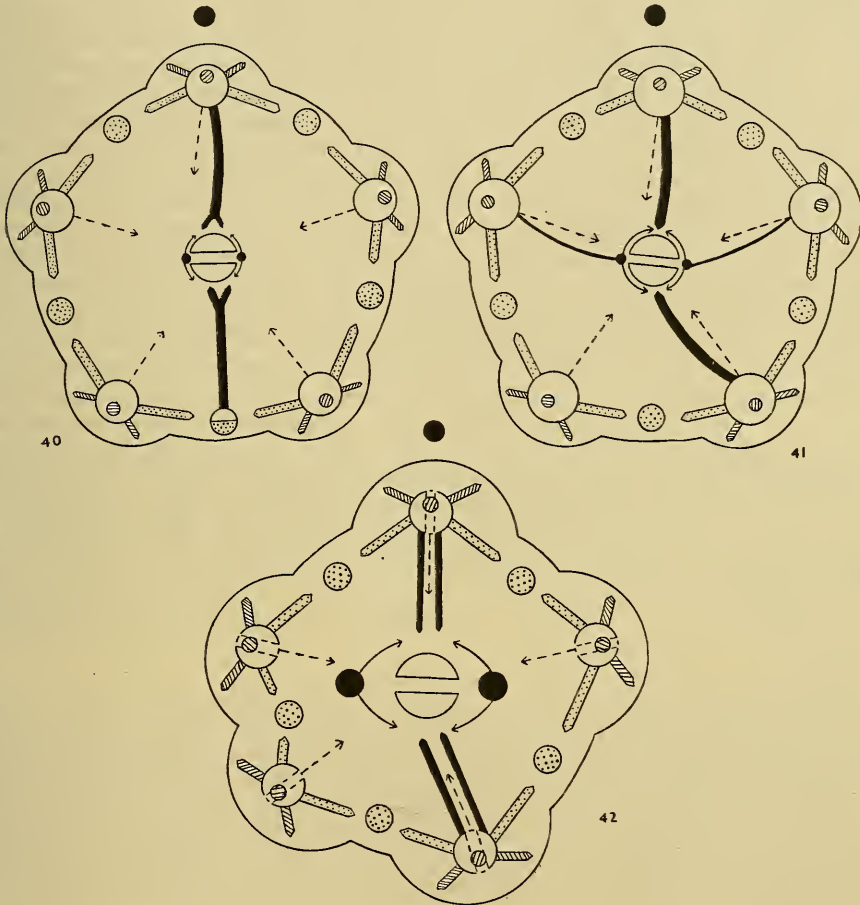
Text-figures 40-42. Derivation of vascular bundles at the ovary dome.

40. *Goodenia* group. 41. *Dampiera group* (in *Anthotium* the ps.-carp. lateral are united to a sepal bundle). 42. *Leschenaultia*. //// Sepal Traces, ˙.˙. Petal Traces, — — — Stamen Traces, ● Carpel Traces.

S. fasciculata Benth. and *S. helmsii* Pritzel.—These species have type (iii) ovary. Their floral structure is more comparable to that of *Verreauxia*. Not only is the structure of the ovary the same, but a spur is present containing the nectary which is not situated on the top of the ovary as in the other Scaevolas.

DIASPASIS.

D. filifolia R.Br.—The only species described to date in this genus. The floral structure is similar to that of *S. albida*. No ribs are present on the surface of the pseudo-ovary and there is no pocket or spur containing a nectary. The stylar supply is derived in the same way as that of *S. hookeri*. The anterior pseudocarpellary dorsal bundle is free for the greater part of the pseudo-ovary wall (Fig. 35).

LESCHENAULTIA.

L. biloba Lindl.—Externally the pseudo-ovary has four ribs, one of which is larger than the others and is shallowly grooved. Ten bundles diverge from the receptacular stele almost at the same level, three of these passing into the smaller ribs, four into the grooves between them and three into the large rib. This large rib appears to be the result of the confluence of two ribs and the groove between. If this is accepted the derivation of the vascular supply of the various floral organs at the ovary summit is similar to that found in the preceding species with the exception of the stylar supply (Fig. 7, 8, 36, 42). The bundles on the sepal radii very often become split into two (Fig. 7); this division is closed up again before the divergence of the bundles at the ovary dome except for the pseudocarpellary dorsals. These diverge from the posterior and an anterior lateral bundle on sepal radii, as double structures (Fig. 7, 42). They remain separate, passing on into the style as distinct bundles. The bifurcations of the lateral bundles provide eight separate strands in the style (Fig. 24-26). The remains of the receptacular stele resolve into two bundles which pass laterally and remain at the junction of the septum and ovary wall. These are the placental supply (Fig. 8) and apparently also represent the pseudocarpellary laterals of the other genera as they continue on above the level of ovular insertion and bifurcate at the base of the style (see above). The ovary does not quite correspond to the generalized form. The "bilocular" zone is well developed and the ovules are inserted in it; just beneath the style the septum splits and a "unilocular" condition is found, which continues on into the style, and there is no uppermost "bilocular" zone. The style is hollow and even open to the exterior via the indusium. Another very peculiar condition is evident in the pseudo-ovary wall. A definite space is present opposite the four bundles on petal radii contained within the grooves. This space separates the tissue surrounding the bundle from the (?) ovary wall proper. The space does not communicate with the exterior at all as it is closed over above; there is no question of its being nectiferous (Fig. 7, 8, 36).

L. linearioides DC., *L. divaricata* F. Muell., and *L. formosa* R.Br. are essentially the same as the preceding species.

ANTHOTIUM.

A. rubriflorum F. Muell.—The derivation of the vascular supply in the receptacle is similar to that found in the Goodenias. The placental supply is a single strand which provides pseudocarpellary laterals whilst still in the receptacle. There are five ribs on the wall of the pseudo-ovary and three deep spurs on the anterior petal radii (Fig. 5) and two much smaller ones on the posterior petal radii. The derivation of the vascular supplies from the bundles of the pseudo-ovary wall is similar to that of *Leschenaultia*. The main difference is to be found in the ovary supply. One pseudocarpellary dorsal diverges from the posterior sepal bundle close to the ovary summit, the other diverges from one of the anterior-lateral sepal bundles low in the pseudo-ovary wall and for the greater length of this latter it is free (Fig. 7). The staminal bundles also diverge from the corresponding sepal bundles, low in the pseudo-ovary wall. The two pseudocarpellary dorsals fuse with the bifurcations of the pseudocarpellary laterals to produce a two-strand condition in the style (Fig. 16, 17, 20). It should also be noted that the bundles on the sepal radii in the pseudo-ovary wall do not split, nor are the pseudocarpellary dorsals double as in *Leschenaultia*.

DAMPIERA.

With regard to floral structure there are two main types within this genus: (i) "bilocular" ovary with one ovule per loculus, (ii) "unilocular" ovary with a solitary ovule. Unfortunately no satisfactory material of the former was obtainable.

D. stricta R.Br.—This species is a member of the latter group. In spite of the term "unilocular" usually applied to this ovary it shows the generalized form, although considerably modified basally. The posterior pseudocarpel is solid (Fig. 6, 38, 45) for most of the basal zone. Immediately above the insertion of the single, anterior ovule,

this pseudocarpel becomes hollow and then the septum aborts, leaving the "unilocular" condition. Just beneath the style the "bilocular" condition is regenerated. There are five ribs on the wall of the pseudo-ovary, each rib corresponding to a sepal. Within these ribs, moreover, there are three vascular bundles, a main one and two lateral ones which are derived from the former low down. The main one divides at the ovary dome to give rise to the staminal strand and two petal laterals each. The posterior and one of the anterior lateral ones further give rise to the two pseudocarpellary dorsals (Fig. 41, 45). There are small nectiferous pockets opposite the grooves, which latter also contain a bundle outside the pocket, which passes directly into the petal. Brough is in error when he states that the nectaries are opposite the stamens. The derivation of the main bundles of the pseudo-ovary wall within the receptacle is similar to that seen in *Scaevola*. The remnants of this stele resolve into a single strand also as in *Scaevola* which passes upwards into the placenta. At the point of ovular insertion this bundle divides into three, one bundle to the ovule and the other two passing outwards to fuse with the posterior lateral bundles on the sepal radii (Fig. 6, 45). These, presumably, are the pseudocarpellary laterals. Evidence is provided for this by the distribution of vascular bundles to the stylar base; in addition to the pseudocarpellary bundles mentioned above the two posterior-lateral sepal bundles distribute a strand each to the base of the style. These strands bifurcate and fuse with the other two as indicated in Figures 16, 17, 41, giving a two-strand structure to the style (Fig. 20).

The insertion of the ovule and abortion of the solid pseudocarpel take place so close to the base that an impression of basal insertion is conveyed.

D. spicigera Benth.—Generally very similar to the preceding species, but the solid pseudocarpel is continued further up the wall of the ovary conveying the impression of lateral insertion. This is characteristic of the section *Linschotenia*.

D. purpurea R.Br.—Similar to *D. stricta*. The petal lateral bundles are free for the greater length of the pseudo-ovary wall and lie beside the sepal laterals in the rather obscure sepaline ribs.

BRUNONIA.

B. australis R.Br.—This species has a superior ovary and hypogynous, epipetalous stamens. Sepal, petal and stamen strands are all derived separately from the receptacular stele and do not fuse. The carpellary supply consists of two dorsals which diverge next, anteriorly and posteriorly, and the single strand resolution of the remnants in the septum. This latter passes directly into the ovule. The style is supplied directly by the dorsal strands without further division or fusion. The style is therefore two-stranded, although different in derivation from any of the other two-strand styles found in this family. The ovary shows a basal "bilocular" zone with the solitary ovule inserted on the short septum. There is no uppermost "bilocular" zone and most of the ovary is aseptate (Fig. 39, 45).

DISCUSSION AND CONCLUSIONS.

These results are summarized in diagrammatic form in Figures 31–42 and 44 which can be used as a basis for discussion.

The structure of the individual floral whorls follows the general pattern found in the Angiosperms with the exception of the ovary. Sepals and petals are, in the more primitive forms, supplied by a single bundle which divides into three, one main and two laterals. This is somewhat obscured, due to vascular condensation in the more advanced genera, but is clear in *Velleia*. In almost all genera examined the ovary can be divided into the three zones mentioned under *Velleia*. It is in vasculation of the ovary that a rather peculiar situation is found. The presence of sterile strands in the placental septum has to be explained, and the fact that the stylar vascular supply is not in the position that one would expect if the locules corresponded to carpels is also anomalous. Nevertheless, the situation can be explained in terms of the classical theory provided that the locules are considered to be derived from two carpels and not one.

The ancestral form of the Goodeniaceae is postulated to have had four carpels in the four lateral positions, each with five vascular strands, a dorsal, two laterals and two ventrals (Fig. 42). Concomitant with the abortion of the septa on the anterior-posterior axis there have been fusions of the vascular bundles as shown in Figure 43. This gives the four-strand condition of the *Velleia* ovary with a central placental supply; the two bundles from the original lateral septa, however, are sterile and diverge as the sterile septal bundles (Fig. 44). At the base of the style the vascular supply rearranges so that the four ancestral carpels are represented by one single strand each (Fig. 11, 12) in some forms or by varying numbers of strands in others (Fig. 21–25). Thus it is postulated that the pseudocarpellary dorsal bundles are, in fact, double or quadruple bundles, a conclusion supported by their bifurcation at the base of the style
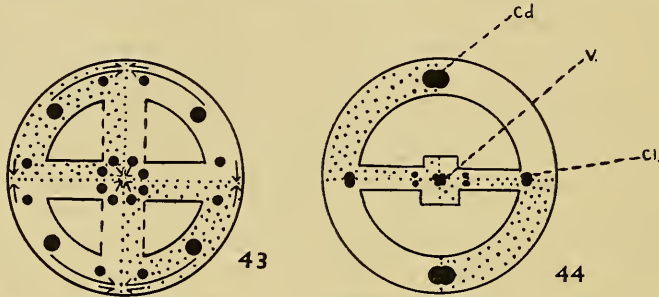
Text-figure 43. 4-locular ancestral ovary showing fusions of vascular bundles (in the phylogenic sense) to produce the Goodeniaceous ovary.
Text-figure 44. Ovary of Goodeniaceae, basic type.

and possibly by their twinned nature in *Leschenaultia* (although in this latter case it may be simply a reflection of the double nature of their parent bundles). It is considered that the ovary of this family has achieved a bilocular condition by fusion of carpels two by two and subsequent condensation of their vasculations rather than by simple abortion. Further development within the family has occurred by the acquisition of a virtually unilocular condition (along at least two different lines), reduction in ovular number and further condensation in the vasculation.

Before considering the relationships of the various genera it may be profitable to consider the question of the inferior ovary in the family. This question really involves much more than can be dealt with satisfactorily here. Puri (1952) has thrown some doubt on the usefulness of the vascular pattern in determining the nature of the pseudo-ovary wall. Douglas has attempted to counter this, but does not appear to have invalidated Puri's arguments entirely. Both of these workers have useful, although different, ways of looking at the same problem. It seems that the ovary of the Goodeniaceae becomes inferior by virtue of fusion of the outer floral whorls to the ovary wall (in the phylogenetic sense) which is here defined as due to relatively superficial mass growth in the ontogenetic sense. The similarity of the structure of the ribs on the pseudo-ovary wall and the sepals which continue them has been remarked upon in connection with *Goodenia*. The resemblance is even more striking in the case of *Dampiera stricta* where both ribs and sepals contain many sclereids, but the petals and the receptacle do not, and the ribs contain the same vascular pattern as the sepals. The presence of a single spur in those genera allied to *Goodenia* and several spurs in *Anthotium* also indicate that superficial zonal growth only is involved, otherwise the position of the spur would be closer to the ovary summit and one could probably expect some inversion of vasculation in this region. Likewise the spaces in the pseudo-ovary wall of *Leschenaultia* are most easily interpreted as incomplete fusion of the petals to the ovary wall, possibly a number of closed spurs. The ribs of the pseudo-ovary of *Goodenia scapigera* likewise are most easily interpreted as incomplete fusion of the sepals to the inner floral whorls. Lastly there is the phylogenetic sequence from *Velleia* through *Symphyobasis* to *Goodenia* which is most easily interpreted as increasing

fusion of floral whorls or increasingly early onset of coalescence of growth areas in ontogeny. There is no internal evidence with respect to *Selliera*, *Scaevola* or *Diaspasis*, but it is reasonable to suggest that the inferior ovary in the case of this family has arisen by superficial zonal growth, although there is the possibility that this growth zone may move into the inner parts of the receptacle as evolution progresses. The difference between the two theories postulated to explain the floral tube and the pseudo-ovary wall becomes smaller when it is considered in this light.

Four main lines of development in the family may be distinguished. *Brunonia* stands somewhat apart and, indeed, has been elevated into a monotypic family. The hypogynous position of the stamens and the very reduced nature of the ovary, separate it from other genera. The former condition may be looked upon as primitive, whereas the latter may be considerably advanced. The different nature of the style vasculation has been remarked upon above. Primulaceae and Gentianaceae have both been mentioned as possible ancestors for this genus, but the generalized structure conforms fairly well with that of the rest of the family.

Velleia shows a certain amount of fusion between floral whorls at the base of the flower, the inner floral parts being united to the ovary to a higher level than the outer ones. This fusion is carried still higher in the flower in *Symphyobasis*, and in *Goodenia* the sepals are fused often almost to the ovary dome. *Calogyne* is a differentiate from *Goodenia* with divided indusia. *Selliera* is also a differentiate from *Goodenia*, distinguished on the fruit and corolla. *Pentaptilon* and *Catosperma* may be representatives of this line with pendulous ovules. In some species of *Goodenia* the number of ovules is reduced to two and in *Verreauxia* to one with a concomitant increase in the size of the "unilocular" medial zone of the ovary (see Fig. 31–33, 45). The presence and position of the single spur and the derivation of the pseudocarpellary dorsals from posterior sepal and anterior petal strands are also characteristic of this group. *Scaevola* is also considered to be a member of this group in which the spur has been lost. The vascular pattern is still essentially the same except in the case of *S. ramosissima*, although the condensation of the vasculation is particularly noticeable. There is no separate derivation of petal laterals and staminal strands from the receptacular stele as in the other members of the *Goodenia* group, and the bundles only separate at the ovary dome. Thus *Scaevola*, in general, exhibits more complete and presumably more efficient fusion than the rest of the group. *Leschenaultia* tends to stand even further apart from the rest of the family than *Brunonia*. The vasculation is, in many instances, quite different from any other member, as has been indicated above. The derivation of the pseudocarpellary dorsals and the presence of three large, closed spurs may indicate a relationship with the next group, but in other respects, notably the hollow style and the structure of the indusium (Carolin, unpub.), it is even more divergent.

Anthotium and *Dampiera* have much in common and are quite different from the other groups. The derivation of the pseudocarpellary dorsals and the presence of several spurs distinguish them from the *Goodenia* group, and the ribs on the pseudo-ovary wall and the placental supply separate them from *Leschenaultia*, in addition to the more orthodox characters. *Anthotium* shows considerable fusion between whorls, but the vasculations of the different organs tend to remain more or less separate, at least in the upper part of the pseudo-ovary (Fig. 45, 37). In *Dampiera* the ovular number and the size of spurs are reduced. In addition, the condensation of the vascular supply is more evident than in *Anthotium* (Fig. 45, 38), and the ovary becomes "unilocular" by reduction of the basal "bilocular" zone and solidification of one "loculus".

It is evident that the scheme of affinities put forward by Krause (1912) has to be considerably modified in the light of this investigation.

Extrapolating these characters, an ancestral form can be suggested (Fig. 45). It was presumably pentamerous except for the gynoecium which consisted of four united carpels; the petals were united into a tube as in *Brunonia* and the sepals were free. From this, *Brunonia* has developed by the reduction of the ovary (possibly in the same manner as the other genera, although equally possibly by simple abortion of two

carpels).   The other genera have developed after a slit appeared in the corolla and further development has been along the usual lines of ovular reduction, gradual increase in union between floral parts and condensation of their vascular systems.   On these
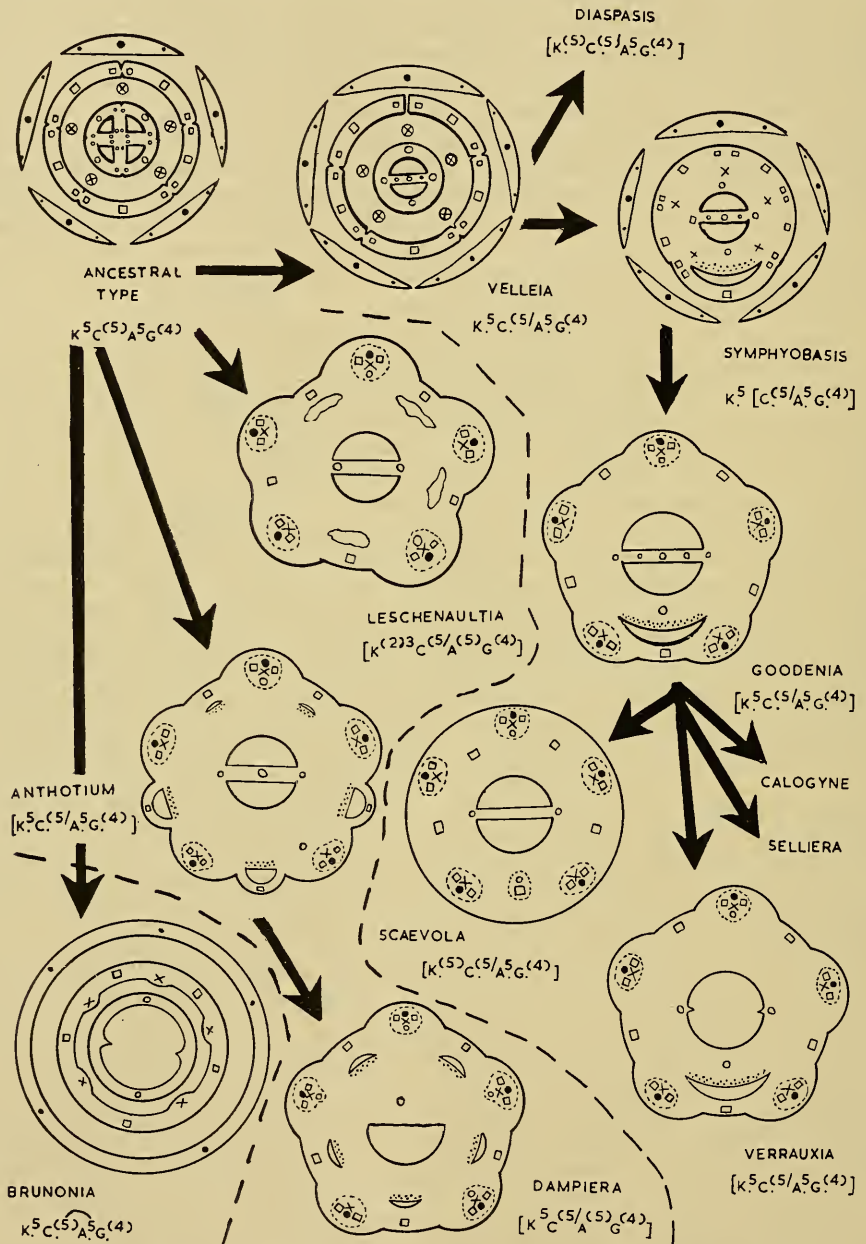
Text-figure 45.   Phylogeny of floral types in the Goodeniaceae.
● Sepal Traces; □ Petal Traces; ✕ Stamen Traces; ◯ Carpel Traces.

results it is impossible to suggest any relationships between this family and any other modern groups.   The pollinating mechanism would appear to be the connecting link between Goodeniaceae and Campanulaceae, and it is hoped to make this the subject of a separate paper.

If these phylogenetic schemes bear examination from other quarters, the family, in the wide sense, may be divided into the following subfamilial groups: (i) GOODENIA group: *Velleia, Symphyobasis, Goodenia, Calogyne, Selliera, Verreauxia, Diaspasis, Scaevola (Pentaptilon* and *Catosperma)*; (ii) LESCHENAULTIA group: *Leschenaultia;* (iii) DAMPIERA group: *Anthotium, Dampiera;* (iv) BRUNONIA group: *Brunonia.* Cytological evidence (Martin, Peacock, Carolin, all unpub.; Jackson, 1958) and other morphological observations all tend to support this conclusion.

These results also suggest that certain generic limits may need revision. *Calogyne berardiana*, as it differs so little from Goodenias and as its style can no longer be considered to be characteristic, should probably be returned to *Goodenia*. *Scaevola fasciculata* and *S. helmsii* should probably be referred to *Verreauxia*.

Acknowledgements.

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